CROSS-SEASONAL EFFECTS ON REPRODUCTIVE PERFORMANCE OF PACIFIC BLACK BRANT

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A

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ABSTRACT

We used re-sightings of Pacific Black Brant from San Quintin Bay, Ojo de Liebre Lagoon, and San Ignacio Lagoon, Baja California and Boundary Bay, British Columbia, to examine winter population structure, variation in structural size and the importance of winter location to individual reproductive performance at the Tutakoke River colony. Sexes of adults and juveniles were distributed equally among winter locations. Adult structural size and mean age were similar among winter locations. A higher proportion of juveniles over-wintered in San Quintin Bay and Ojo de Liebre Lagoon. Individuals wintering at Ojo de Liebre and San Ignacio lagoons were less likely to breed and initiated clutches later than those that wintered in Boundary Bay or San Quintin Bay. Maternal mass did not vary, although clutch size was slightly larger in individuals that wintered in southern areas. Variation in winter location and habitat quality could influence individual reproductive performance and population dynamics.

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ACKNOWLEDGEMENTS

Both chapters of this Masters of Science thesis are written in journal format in preparation for submission. Chapter 1 is intended for submission to *The Condor* and Chapter 2 for submission to *The Auk*. This thesis is single authored, although co-authors for each manuscript are referenced on the first page of each chapter. The "we" in each chapter refers to all authors referenced.

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INTRODUCTION

Female geese use nutrient reserves acquired outside the breeding season for migration and reproduction (Ankney and MacInnes 1978, Raveling 1979, Wypkema and Ankney 1979, Tuenissen et al. 1985, Gauthier et al. 1992). Spring condition upon arrival to the breeding grounds influences clutch size and reproductive success in most arctic-nesting goose populations (Ryder 1970, Ankney and MacInnes 1978, Raveling 1979). Storage of nutrient reserves begins on the wintering grounds (Wypkema and Ankney 1979, McLandress and Raveling 1981, Gauthier et al. 1992); thus, variation in winter habitat quality may influence spring condition of females, leading to variation in individual fitness and, in turn, population dynamics.

Many studies of a number of migratory species indicate that distribution during winter months is related to age, sex, social status, or structural size (Ketterson and Nolan 1976, Ketterson and Nolan 1983, Prescott 1994, Alisauskas 1998, Cristol et al. 1999). A particular winter location likely exposes an individual to varying environmental conditions and social interactions that may influence its subsequent breeding and survival (Cristol et al. 1999). Spatial variation in winter habitat quality, therefore, may influence individual condition in winter and consequently reproductive performance.

Earlier studies have used regression approaches to link indices of winter habitat quality with reproductive success in populations of Mallards (*Anas platyrhynchos*) and Pintails (*Anas acuta*) (Heitmeyer and Fredrickson 1981, Raveling and Heitmeyer 1989). Difficulties in following individuals throughout their annual cycle, however, have made it

difficult to examine the relationship between winter location and components of subsequent individual reproductive performance and influences on population dynamics. Our collaborative effort with the Alaska Biological Science Center of the U. S. Geological Survey following color-marked Pacific Black Brant (*Branta bernicla nigricans*) throughout their annual cycle enabled us to examine winter population structure and directly link individual reproductive performance with associated winter locations.

Pacific Black Brant winter along a latitudinal gradient in subtidal and intertidal areas along the Pacific Coast of North America (Bellrose 1980, Reed et al. 1998a). Approximately 75% of the total population winters in Mexico, with nearly half of the total population wintering in embayments on the west coast of Baja California; the remainder of the population winters in bays along the Pacific Coast of the United States and Canada from Alaska to California (Sedinger et al. 1993).

Mid-winter surveys show that a shift in winter distribution in Baja California has occurred since the 1960's; for unknown reasons, brant are shifting northward toward San Quintin Bay where they are harvested and population densities are higher (Conant et al. 1998). Changes in winter distribution in other goose populations have been adaptive responses to differential harvest pressure, survival, or changes in food abundance (Kirby and Obrecht 1982, Raveling 1978, Wilson and Atkinson 1995, Ebbinge 1991). Thus, shifts in winter distribution of brant, such as in Baja California, may be in response to variation in winter habitat quality (Bellrose 1980, Kirby and Obrecht 1982, Vickery et al.

1995, Summers et al. 1996) or represent a shifting balance between survival and fecundity (Raveling 1978).

Pacific Brant are unique among geese in that winter diet is comprised almost entirely of relatively low quality seagrasses and marine algae (Einarsen 1965, Ward and Stehn 1989). Feeding opportunities are tidally influenced and restricted to the daylight period (Kramer et al. 1979, Ward and Stehn 1989). Evidence suggests that food availability may decline with decreasing latitude in Baja California, and that food quality may vary among years (D. Ward unpubl. data). Feeding constraints and poor-quality diet (Reed et al. 1998a), may limit storage of nutrient reserves necessary for reproduction in some individuals. Thus, variation in habitat quality may influence winter condition, leading to variation reproductive performance among individuals from different wintering locations.

We observed uniquely marked individuals breeding on the Tutakoke River colony on the Yukon-Kuskokwim Delta, Alaska, who had been re-sighted at the following wintering locations: Boundary Bay, British Columbia; San Quintin Bay, Ojo de Liebre Lagoon, and San Ignacio Lagoon, Baja California, to compare reproductive performance among individuals and examine winter population structure. Female condition was estimated by using an index of maternal mass at hatch. We also assessed the relationship between winter location and initiation date, clutch size, and probability of breeding.

CHAPTER 1. GEOGRAPHIC VARIATION IN POPULATION STRUCTURE AND BODY SIZE OF WINTERING PACIFIC BLACK BRANT[1]

INTRODUCTION

Individuals of different age-sex classes in many species of migratory birds tend to segregate during winter (Ketterson and Nolan 1983). Males have a propensity to winter closer to breeding areas or farther north than females (King et al. 1965, Ketterson and Nolan 1976, Nichols and Haramis 1980, Alexander 1983, Morton 1984, Myers 1981, Prescott 1991). Spatial segregation of age classes, however, is less consistent and varies among species (Ketterson and Nolan 1983). Winter location likely influences the exposure of individuals to environmental conditions and social interactions that could impact survival, future breeding, and gene flow (Cristol et al. 1999).

Sex-specific variation in distribution of waterfowl in North America during winter has been described in some duck species (Hepp and Hines 1991). Band recovery data of Canvasbacks (*Aythya valisineria*) and Christmas Bird Counts for Canvasbacks and Ring-necked ducks (*Aythya collaris*) indicate that males occur farther north than females during winter (Nichols and Haramis 1980, Alexander 1983). An aerial photographic census of wintering Canvasbacks along the Atlantic coast also recorded latitudinal variation in the sex ratio, with males most numerous in northern areas (Haramis et al. 1985). Conversely, sex-specific variation in winter latitude has not been observed in Mallards (*Anas platyrhynchos*), Black Ducks (*Anas rubripes*), or Wood Ducks (*Aix*

[1] Prepared for submission to the *Condor* as Schamber, J. L., J. S. Sedinger, D. H. Ward, and K. R. Hagemeier. Geographic variation in population structure and body size of wintering Pacific Black Brant.

sponsa) (Nichols and Hines 1987, Diefenbach et al. 1988, Hepp and Hines 1991), respectively. Some evidence exists, however, for age-specific variation in wintering distributions of Mallards and Wood Ducks, although the pattern was weak and inconsistent in direction among years for Mallards and age-specific segregation was observed only in a small population of Wood Ducks (Nichols and Hines 1987, Hepp and Hines 1991).

Most descriptions of latitudinal variation in geese during winter have been limited to populations from different breeding locations (Lefebvre and Raveling 1967, Craven and Rusch 1983, Reed et al. 1989, Ely and Takekawa 1996). Close association of family members and breeding pairs outside the breeding season (Boyd 1953, Prevett and MacInnes 1980, Reed 1993, Warren et al. 1993) may limit the potential for age- or sex-related segregation during winter. Difficulty in remotely discerning sex and age (Bellrose 1980) of wintering adult geese decreases the ease of quantifying spatial structure of wintering populations. Re-sightings of color marked geese during winter, however, allow determination of population structure and annual variation in distribution (Samuel et al. 1991).

Black Brant (*Branta bernicla nigricans*) (hereafter brant) are distributed along a latitudinal gradient outside of the breeding season, wintering in coastal areas from the Alaska Peninsula to Mexico (Bellrose 1980, Reed et al. 1998a). For brant breeding on the Yukon-Kuskokwim (Y-K) Delta, migratory distance for individuals wintering in British Columbia, Canada is approximately 2,300 km less than for individuals wintering in southern Baja California, Mexico. Accordingly, variation in proportions of age and

sex classes may exist among these wintering populations. Mean structural size of adult individuals in each sex class also may vary among winter locations.

Expectations of equal distributions of sexes among wintering areas are relevant in brant, because observations of small-bodied geese indicate a tendency for mated individuals to loosely associate in larger winter flocks (Johnson and Raveling 1985). However, juveniles of such species appear to dissociate from family members (Johnson and Raveling 1985), although Reed (1993) reported cohesion of some family groups in brant during winter in northern locations.

Nevertheless, annual survival is lower in juvenile brant than in adults (Ward et al. in review, Sedinger et al. 1997), suggesting that juveniles may survive migration less well. Therefore, selection might favor shorter migration by juvenile brant. On the other hand, selection against juveniles that migrate farther might cause variation in age ratio but would not reflect a 'choice' made by the birds themselves.

Geographic variation in body size exists in many avian species due to variation in percent of age-sex classes (Cristol et al. 1999), but few studies have concentrated on variation among areas in body size of particular age-sex classes (Prescott 1994). Evidence in Lesser Snow Geese suggests that smaller-bodied individuals winter farther north than larger individuals, potentially due to the inability of smaller individuals to migrate longer distances (Alisauskas 1998). Brant may exhibit similar patterns during winter, given the great distances among various winter locations.

Re-sightings of color-marked Black Brant throughout the year permitted us to associate breeding individuals with known winter locations, allowing direct investigation

of population structure and variation in body size during winter. We used re-sighting data of individuals banded at the Tutakoke River colony on the Y-K Delta to examine winter distribution of each age-sex class in Pacific Black Brant and geographic variation in body size of adult brant.

METHODS

STUDY AREAS

Breeding area. Brant nest in wet sedge meadows on the Tutakoke River colony, located near the confluence of the Tutakoke and Kashunuk Rivers (61° 15'N, 165° 37'W) in the Yukon Delta National Wildlife Refuge (see Sedinger and Flint 1991 for description of study area). Approximately 6,500 breeding pairs nest at the Tutakoke colony and >30% of these individuals are marked. Marked individuals were identified and assigned to winter locations through observations (re-sightings) of alphanumerically encoded color tarsus bands using variable-power spotting scopes from arrival of brant through the end of nesting.

Adults and goslings were captured in corral traps (Cooch 1953) during adult remigial molt in 1986-1999. Individuals were subsequently fitted with a metal U. S. Fish and Wildlife Service tarsus band and a uniquely coded alphanumeric plastic color tarsus band. Culmen and tarsus were measured on captured individuals (± 0.1 mm) using dial calipers. Mass (± 10 g for adults and ± 5 g for goslings) was measured using spring scales. Individuals captured or observed at the Tutakoke colony and re-sighted from approximately late fall through early spring of 1997/98-1999/2000 were included in our study.

Wintering areas. Approximately 75% of the brant population winters in embayments of Mexico from Baja California to Sinaloa, with half of the total population wintering on the Pacific coast of Baja California (Conant et al. 1998). The remainder of the population winters in bays along the Pacific coast of the United States and Canada from California to Alaska. Brant were identified during winter months through re-sightings of alphanumerically encoded color tarsus bands using variable-power spotting scopes. Brant were re-sighted by staff of federal, state and private agencies, as well as private individuals at seven distinct winter locations during the three years of this study: San Quintin Bay (30° N, 115° W), Ojo de Liebre Lagoon (27° N, 113° W), San Ignacio Lagoon (26° N, 112° W), Baja California; Morro Bay (35° N, 120° W) and Humboldt Bay, California (40° N, 124° W); Willapa Bay, Washington (47° N, 124° W); and Boundary Bay, British Columbia (49° N, 120° W). No re-sighting attempts were made in Ojo de Liebre Lagoon in winter of 1997-98.

Because brant undergo protracted migratory movements to their ultimate wintering areas and during spring migration (Einarsen 1965, Dau 1992, Reed et al. 1998a), we examined when movements among specific wintering areas were most stable, indicating brant in a given locale had reached their final winter location or when spring migration was initiated. We used individuals that were re-sighted in more than one area during winter to track migratory movements among winter locations. We totaled the number of new re-sightings that occurred over ten-day blocks of time for each location throughout the winter months. Proportions of new re-sightings appearing during each ten-day block were then plotted for each winter location. Because of continuous re-

sighting effort throughout a ten-day period, within a winter location, the relative fluctuation in number of new bands observed was used as an indicator of movement among areas. Consecutive ten-day periods with relatively few new band observations (approximately 10% or less of total bands observed) within a location were indicative of minimal movement into that area. The beginning and terminal dates of these periods were set as bounds for the wintering period in a specific location. Individuals observed between these bounds were classified as having wintered in that location. Using these criteria, we were able to define distinct wintering periods consistent among years for four locations in this study: 1 November to 5 February for Boundary Bay, 8 December to 5 February for San Quintin Bay, and 7 January to 16 February for Ojo de Liebre and San Ignacio lagoons. Individuals re-sighted in these locations during the defined wintering period were included in the analyses.

STATISTICAL ANALYSES

We used a log-linear model and maximum likelihood ratio chi-square test of significance (PROC CATMOD; SAS 1999) to determine if sex-specific distribution of adults or juveniles was independent of winter location and year. We did not have data for all four-winter locations in every year; therefore, we did not include the interaction of winter location and year in the analysis. Adults and goslings approximately 30 days of age captured at Tutakoke and re-sighted the following winter were included in the analysis. We determined proportions of each sex (PROC FREQ; SAS 1999) at each winter location and present results of this analysis by wintering location and age class.

We compared mean age of individuals from different wintering locations across years and between sexes using the general linear model procedure of SAS (1999). We included only known-age brant, initially classified as goslings or one-year olds, based on plumage (Bellrose 1980), in late summer captures, and re-sighted the following winter.

To test the hypothesis that relative proportions of juveniles and adults were independent of year and winter location, we used a log-linear model and maximum likelihood ratio chi-square test of significance (PROC CATMOD; SAS 1999). We could not include the interaction of winter location and year because we did not have observations from all four-winter locations in all years. Individuals observed in each winter location were classified as either juveniles, if they had been banded as a gosling the previous summer, or adults if they had been banded as a one year-old the previous summer or earlier as adults.

Variation in linear measures, culmen and tarsus, was compared among adults from known winter locations among years and between sexes using an analysis of variance (PROC GLM; SAS 1999). Assuming structural size does not change once individuals become adults (Sedinger et al. 1995), we included post-breeding adults (≥ 2-years-old when measured) in our analysis. To avoid violating assumptions of independence, we calculated mean measurements of individuals captured in multiple years and used the mean in our analysis.

To control for variation in body size, we performed principal component analysis (PCA) using the correlation matrix of linear measures (culmen and tarsus) (PROC PRINCOMP; SAS 1999) to construct the first principal component (PC1) as an index to

body size (Alisauskas and Ankney 1987). We then examined variation in PC1 scores among individuals from different winter locations in a general linear model (PROC GLM; SAS 1999) that included year and sex as sources of variation.

For portions of our analyses, we used an information-theoretic approach to assess multiple statistical models. For analyses using least squares method of estimation in a general linear model, we generated a list of *a priori* candidate models and selected the most parsimonious model using Akaike's Information Criterion (AIC) (Burnham and Anderson 1998), derived from the estimated residual sum of squares (RSS) specific to a model (Anderson et al. 2000). We used a modified criterion (AIC_c) to adjust for small sample sizes in our analyses (Burnham and Anderson 1998). We generated candidate models from permutations of our most general model. We ranked models by the difference in AIC_c score between top (lowest score) and candidate models. We report Akaike model weights (w_i) as evidence for the best models (Anderson et al. 2000) and as strength of evidence for the importance of a parameter in a model. We could not include models containing interactions of year and sex with winter location in these analyses owing to lack of data for some years or one sex at particular locations.

RESULTS

We examined variation in sex and age structure of the winter population using 955 marked individuals (551 females and 404 males). Of these, 126 were juvenile females and 91 were juvenile males. For adults, females outnumbered males at all winter locations, but relative proportions did not vary among winter locations (χ^2=2.16, df=3, P=0.54; Table 1-1) and among years (χ^2=1.30, df=2, P=0.52). We detected a greater

proportion of females than males at Tutakoke. Therefore, proportions of male and females are not representative of the population, but should be similar among wintering locations if sexes do not segregate in winter. Sexes of juveniles were distributed equally among winter locations (χ^2=3.12, df=3, P=0.37; Table 1-1) and among years (χ^2=3.01, df=2, P=0.22). Proportions of sexes in juveniles indicate a slight trend among winter locations; however, we attribute this to sampling error associated with small sample size in three of the four locations.

Mean age of individuals was best described by differences between sexes as indicated by low AIC_c of Model 1 (Table 1-2). However, Model 2, which included only winter location (Table 1-2), provided some evidence that winter location was important in explaining variation in age of birds. Lower ranked models included year (Table 1-2), suggesting little variation among years. Mean age of breeding birds was lowest in San Quintin Bay and San Ignacio Lagoon as compared to those in Boundary Bay and Ojo de Liebre Lagoon (Figure 1-1).

The proportion of juveniles in the wintering population varied among winter locations (χ^2=12.91, df=3, P=0.005; Figure 1-2), and among years (χ^2=6.24, df=2, P=0.04 Figure 1-2). Higher proportions of young on average wintered in San Quintin Bay (25%) and Ojo de Liebre Lagoon (22%) than in Boundary Bay (14%) and San Ignacio Lagoon (10%) across years.

Structural measurements were obtained for 212 adult males and 318 adult females from known wintering locations. Variation in culmen was best described by differences between sexes as indicated by low AIC_c of Model 1 (Table 1-3). Model weights summed

across the top four models (Σw_i=0.99; Table 1-3), further provide substantial evidence for differences between sexes. Models 2 and 3, which included, either winter location or year, did not compete well with Model 1, as evidenced by low model weights (Table 1-3), providing little explanatory support for these terms. Variation in tarsus also was best described by differences between sexes, as indicated by the low AIC_c of Model 1 and summed model weights of the top four models (Σw_i=0.99; Table 1-4). The model weights for the second- and third-best models indicate some evidence of variation in tarsus among years (w_i=0.34) and winter locations (w_i=0.21) (Table 1-4). Individuals wintering in San Quintin Bay tended to have smaller tarsus measurements than individuals from southern areas in Baja California (Figure 1-3). PC1 was positively correlated with both linear measures and was therefore interpreted as an index of structural size. As expected, differences between sexes best-described variation in PC1 score (Model 1; Table 1-5). The second-best model was also a competitive model and included year, providing moderate support for annual variation in individual size of adults (Table 1-5). Models 3 and 4, although non-competitive, provide weak evidence that PC1 score varied among individuals from different winter locations, as evidenced by relatively low AIC_c and summed model weight Σw_i=0.14 (Table 1-5). Individuals from San Quintin Bay tended to have lower PC1 scores than individuals from southern areas in Baja California (Figure 1-4).

DISCUSSION

SEX-SPECIFIC VARIATION

We found no evidence for sex-related variation in wintering locations of brant. These findings are consistent with distribution patterns of Black Ducks and Mallards (Nichols and Hines 1987, Diefenbach et al. 1988), but differ from other Anatinae and other avian species (Cristol et al. 1999). Similar distributions of male and female brant are also consistent with lack of sex differences in seasonal survival of adults (Ward et al. 1997), suggesting that males and females experience similar conditions during winter (Francis and Cooke 1992).

Geese maintain long-term pair bonds (Rowher and Anderson 1988) whereas species in which sexes segregate during winter are typically seasonally monogamous breeders (Bellrose 1980, Oring 1982). Smaller bodied geese, however, maintain relatively loose pair-bond associations within the same flocks outside of the breeding season (Johnson and Raveling 1985). Brant are among the smallest-bodied geese (Owen 1980), but some pair bond associations have been observed in large aggregations during the winter in Baja California and in British Columbia (D. Ward unpubl. data, Reed 1993).

AGE-SPECIFIC VARIATION

Our models provided some support for an effect of winter location on variation in mean age of adult brant observed breeding at Tutakoke. Our inability to detect substantial variation in age of adult brant among winter locations may have resulted from our restricting the analysis to the breeding segment of the population, because younger adults breed at lower frequency than older adults (Sedinger et al. in press). Adults

wintering in southern Baja California were less likely to breed than those wintering farther north, especially in 1998 (Schamber 2001). Our estimate of age in southern Baja California, therefore, may be positively biased due to the larger proportion of non-breeding individuals, that we did not include in our analysis.

In some ducks, dominance behavior displaces subordinate individuals into sub-optimal areas (Nichols and Haramis 1980, Hepp and Hair 1984). Vangilder et al. (1985) observed that Atlantic brant (*Branta bernicla hrota*) are distributed in winter according to necklace type and suggested social status might contribute to variation in winter location. Individuals of lower social status, who are also non-breeders, therefore, may be relegated to southern locations.

Proportions of juveniles varied among winter locations. This result is consistent with plumage observations (D. Ward pers. obs.) of a larger proportion of juveniles wintering in San Quintin Bay than in other areas in Baja California. Our results indicated that a greater proportion of juveniles wintered in San Quintin Bay and Ojo de Liebre Lagoon than in San Ignacio Lagoon. Our sample size was small for Boundary Bay, British Columbia, however and, therefore, our estimates of proportions of juveniles are imprecise, so inference from this area is limited. If, as Reed (1993) suggested, cohesiveness of family groups is maintained during the winter months, variation in production of young among pairs using different winter locations may explain this distribution. Alternatively, differential migration or early-winter mortality of young may also explain our results among wintering brant. Individuals wintering in Ojo de Liebre Lagoon have the lowest overall probability of breeding among wintering brant and have

later-hatching goslings that likely survive less well (Schamber 2001), suggesting that variation in fecundity cannot fully explain spatial variation in proportion of juveniles. Lambeck (1990) noted in dark-bellied brant (*Branta bernicla bernicla*) a disproportionate number of juveniles in more favorable foraging areas. Density and availability of food declines with decreasing latitude in Baja California (D. Ward unpubl. data). Nutritional quality of food also declines with latitude in Baja California, although this relationship varies among years (D. Ward unpubl. data). San Quintin Bay, therefore, may be a more favorable habitat, despite being the only one of the three areas in Baja California with harvest pressure (Kramer et al. 1979) and hosting the highest density over-wintering population. Dominant family groups (Boyd 1953, Raveling 1970, Black and Owen 1989) may occupy northern wintering locations with more favorable foraging conditions (Raveling 1970, Teunissen et al. 1985, Black et al. 1992) and displace subordinate families and non-breeding individuals to less favorable southern areas. Social interactions, thus, may vary among locations and influence distribution patterns within Baja California.

BODY SIZE VARIATION

Winter location was not important in describing variation in body size among adults wintering at different locations. Similar patterns have been observed in Dark-eyed Juncos (*Junco hyemalis*) and male Evening Grosbeaks (*Coccothraustes vespertinus*) (Ketterson and Nolan 1983, Prescott 1994). A current hypothesis states that, in migratory species, when sex-age classes differ in distribution, individuals of larger size should winter farther north because they are more cold tolerant or because they can better meet

daily energy demands (Ketterson and Nolan 1976). Brant winter exclusively in maritime climates and temperature differences between Boundary Bay, British Columbia and southern areas in Baja California are unlikely to be sufficient to favor size-based spatial segregation. Alisauskas (1998) reports, in Mid-Continent Lesser Snow Geese, that smaller sized-birds winter farther north than larger bodied individuals. We found a similar, although weak, pattern among adult individuals in Baja California. Structurally smaller individuals may not be capable of reaching a 'threshold' level of condition necessary for breeding (Schamber 2001); therefore, we may only detect larger individuals from southern locations in Baja California breeding at Tutakoke.

IMPLICATIONS FOR POPULATION DYNAMICS

Spatial variation in winter distribution of juveniles and segregation according to body size in adults could influence future recruitment and fecundity. Larger individuals are more likely to breed and are more fecund than smaller individuals (Sedinger et al. 1995). Furthermore, individuals that wintered at Ojo de Liebre or San Ignacio lagoons were less likely to breed, compared with individuals from San Quintin Bay, particularly in an El Niño influenced year (Schamber 2001). Although we recognize that our results are merely suggestive of a trend in body size in Baja California, limitation of breeding only to structurally larger individuals in southern areas could negatively influence population growth.

It is likely that juveniles have not reached asymptotic structural growth by their first winter; therefore, variation in food availability and, in some years, food quality in

Ojo de Liebre Lagoon (D. Ward unpubl. data) could influence future size and in turn, future fecundity (Sedinger et al. 1995, Choudhury et al. 1996).

Variation in habitat quality among winter locations may influence future individual fecundity of juveniles over-wintering in southern habitats, potentially influencing population dynamics. Future management and research efforts should focus on variation in winter distribution and mechanisms that determine segregation among winter locations and their influence on population dynamics.

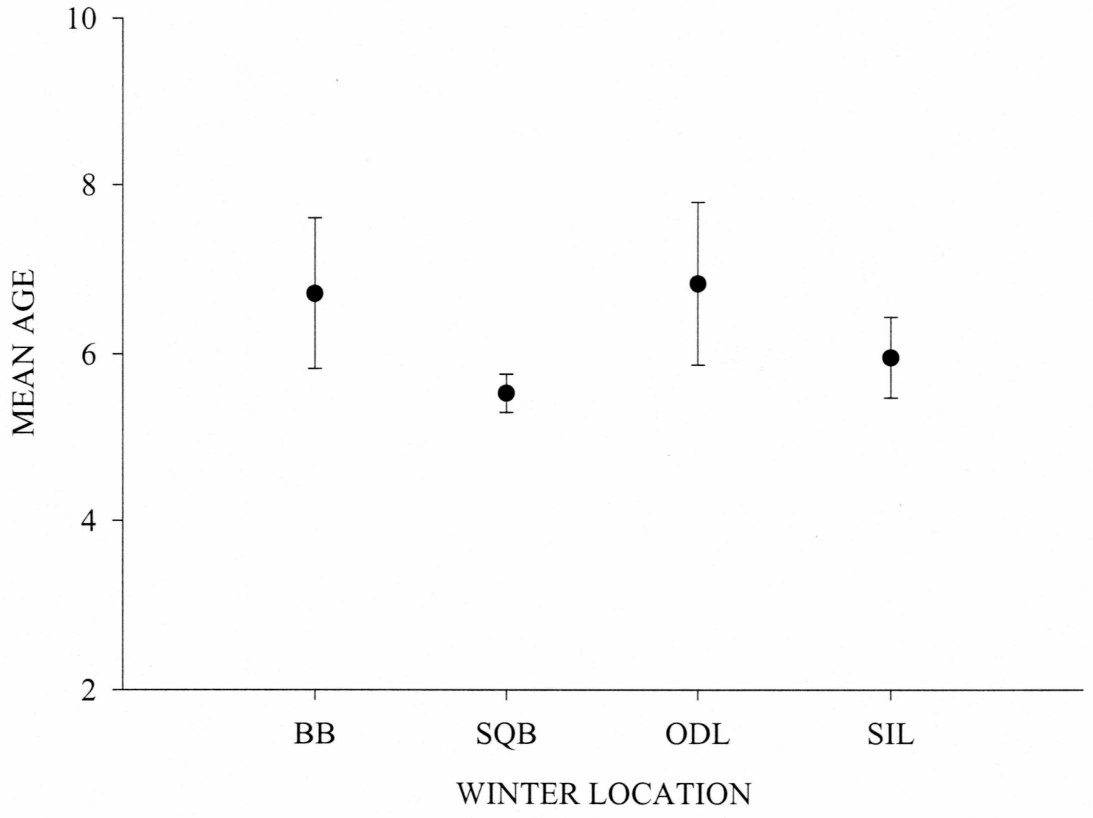

Figure 1-1. LSMean age of Tutakoke-banded breeding birds in each winter location. Winter locations are arranged from north to south and abbreviated as: BB-Boundary Bay, SQB-San Quintin Bay, ODL-Ojo de Liebre Lagoon, and SIL-San Ignacio Lagoon. Error bars represent 1 SE from the mean.

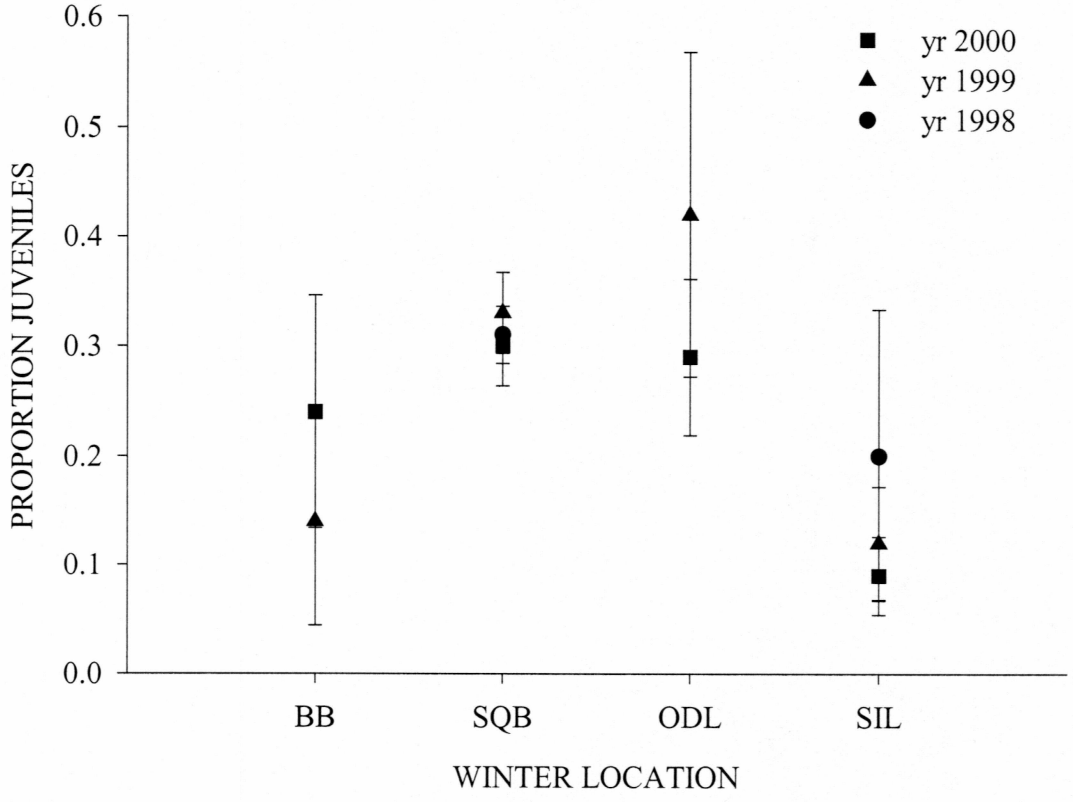

Figure 1-2. Annual proportion of Tutakoke-banded juveniles in each winter location. Winter locations are arranged from north to south and abbreviated as: BB-Boundary Bay, SQB-San Quintin Bay, ODL-Ojo de Liebre Lagoon, and SIL-San Ignacio Lagoon. Error bars represent 1 SE from the mean.

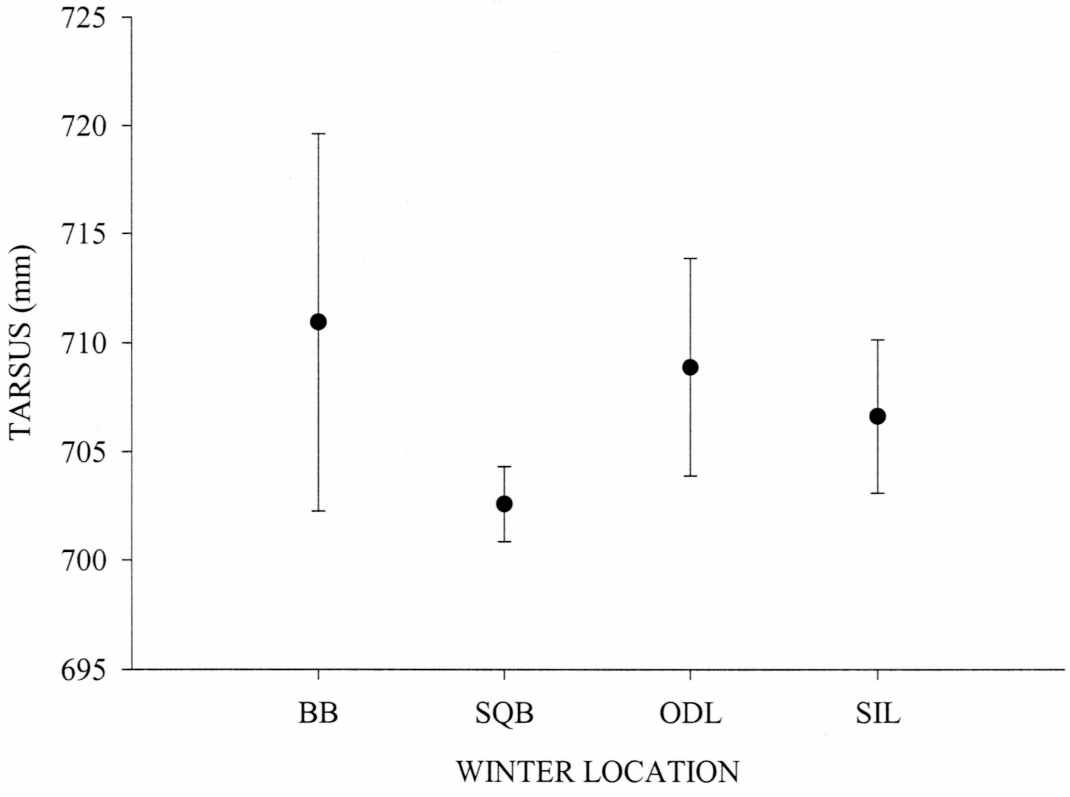

Figure 1-3. LSMean tarsus measure of adults banded at Tutakoke in each winter location. Winter locations are arranged from north to south and abbreviated as: BB-Boundary Bay, SQB-San Quintin Bay, ODL-Ojo de Liebre Lagoon, and SIL-San Ignacio Lagoon. Error bars represent 1 SE from the mean.

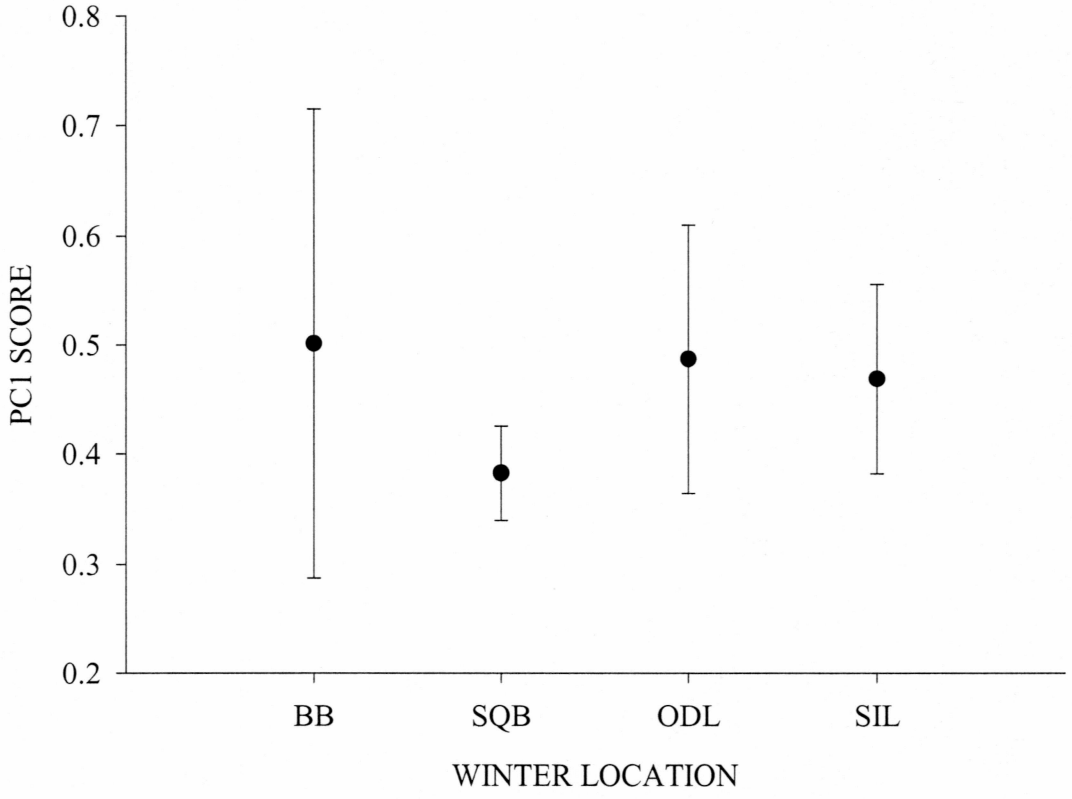

Figure 1-4. LSMean PC1 scores of adults banded at Tutakoke in each winter location. Winter locations are arranged from north to south and abbreviated as: BB-Boundary Bay, SQB-San Quintin Bay, ODL-Ojo de Liebre Lagoon, and SIL-San Ignacio Lagoon. Error bars represent 1 SE from the mean.

Table 1-1. Proportion of sexes of adults and juveniles banded at Tutakoke among winter locations across years.

		Winter Location[a]				
Age	Sex	Boundary Bay	San Quintin Bay	Ojo de Liebre Lagoon	San Ignacio Lagoon	Totals
Adults	Male	0.29	0.30	0.28	0.27	313
	Female	0.71	0.70	0.72	0.73	425
Totals		36	527	60	115	738
Juveniles	Male	0.33	0.41	0.59	0.46	91
	Female	0.67	0.59	0.41	0.54	126
Totals		6	181	17	13	217

[a] Winter locations arranged from north to south.

Table 1-2. Model selection criterion for mean age of brant among winter locations during years 1998-2000.

No. and $Model_i$	SSE_i	K_i	AIC_c	Δ_i	w_i
1. {s}	777.285	3	246.159	0.000	0.500
2. {w}	761.133	5	248.177	2.017	0.182
3. {w s}	756.946	6	248.902	2.743	0.127
4. {y}	780.621	4	249.591	3.432	0.090
5. {y s}	777.121	5	250.401	4.241	0.060
6. {w y}	759.732	7	252.315	6.155	0.023
7. {w y s}	755.176	8	253.042	6.883	0.016

$Model_i$ parameters: s=sex; w=winter location; y=year

SSE_i=residual sum of squares from GLM of $model_i$

K_i=number of estimated parameters for $model_i$

AIC_c=modified Akaike Information Criterion score

Δ_i=difference of $model_i$ AIC_c score and top model (lowest AIC_c score)

w_i=Akaike model weight

Table 1-3. Model selection criterion for culmen of individuals among winter locations during years 1998-2000.

No. and $Model_i$	SSE_i	K_i	AIC_c	Δ_i	w_i
1. {s}	177331.766	3	2873.240	0.000	0.825
2. {y s}	177217.382	5	2877.002	3.761	0.125
3. {w s}	177261.778	6	2879.174	5.933	0.042
4. {w y s}	177151.977	8	2882.999	9.759	0.006
5. {y}	212004.135	4	2962.065	88.824	0.000
6. {w}	212527.789	5	2965.306	92.065	0.000
7. {w y}	211905.004	7	2967.989	94.748	0.000

$Model_i$ parameters: s=sex; y=year; w=winter location

SSE_i=residual sum of squares from GLM of $Model_i$

K_i=number of estimated parameters for $Model_i$

AIC_c=modified Akaike Information Criterion score

Δ_i=difference of $Model_i$ AIC_c score and top model (lowest AIC_c score)

w_i=Akaike model weight

Table 1-4. Model selection criterion for tarsus of individuals among winter locations during years 1998-2000.

No. and $Model_i$	SSE_i	K_i	AIC_c	Δ_i	w_i
1. {s}	428988.676	3	3302.576	0.000	0.375
2. {y s}	425549.155	5	3302.739	0.162	0.346
3. {w s}	424550.783	6	3303.648	1.071	0.219
4. {w y s}	423257.313	8	3306.292	3.715	0.058
5. {y}	618640.465	4	3482.531	179.954	0.000
6. {w y}	615032.648	7	3485.840	183.263	0.000
7. {w}	620939.832	5	3486.376	183.799	0.000

$Model_i$ parameters: s=sex; y=year; w=winter location

SSE_i=residual sum of squares from GLM of $model_i$

K_i=number of estimated parameters for $model_i$

AIC_c=modified Akaike Information Criterion score

Δ_i=difference of $model_i$ AIC_c score and top model (lowest AIC_c score)

w_i=Akaike model weight

Table 1-5. Model selection criterion for PC1 score of individuals from different winter locations during years 1998-2000.

No. and $Model_i$	SSE_i	K_i	AIC_c	Δ_i	w_i
1. {s}	258.364	3	-301.022	0.000	0.556
2. {y s}	256.843	5	-299.817	1.205	0.304
3. {w s}	256.827	6	-297.797	3.224	0.111
4. {w y s}	256.126	8	-294.998	6.024	0.027
5. {y}	392.742	4	-95.461	205.561	0.000
6. {w y}	391.361	7	-91.022	210.000	0.000
7. {w}	394.899	5	-90.757	210.265	0.000

$Model_i$ parameters: s=sex; y=year; w=winter location

SSE_i=residual sum of squares from GLM of $model_i$

K_i=number of estimated parameters for $model_i$

AIC_c=modified Akaike Information Criterion score

Δ_i=difference of $model_i$ AIC_c score and top model (lowest AIC_c score)

w_i=Akaike model weight

CHAPTER 2. EFFECTS OF WINTER LOCATION ON REPRODUCTIVE PERFORMANCE OF PACIFIC BLACK BRANT[2]

INTRODUCTION

Numerous studies have documented that geese rely on nutrient reserves acquired before arrival on breeding areas to aide in migration and reproduction. Ankney and MacInnes (1978) showed that clutch size and incubation constancy in Lesser Snow Geese (*Chen caerulescens caerulescens*) are dependent on adequate stored nutrient reserves obtained before arrival to the breeding grounds. Raveling (1979) also showed that Cackling Canada Geese (*Branta canadensis minima*) rely on stored nutrients for approximately half of the energy they require during egg laying and incubation. Furthermore, nutrient reserves, obtained on spring staging areas, in Dark-bellied Brant (*Branta bernicla bernicla*) in the Dutch Wadden Sea influences reproductive success (Ebbinge et al. 1982, Tuenissen et al. 1985); heavier females return to staging areas with young the following fall.

Lesser Snow Geese begin storing nutrients on the wintering grounds and accumulate additional reserves along the spring migration route (Wypkema and Ankney 1979). Gauthier et al. (1992) suggested that timing of spring migration from the wintering grounds and nutrient reserve accumulation in Greater Snow Geese (*Chen caerulescens atlantica*) occur simultaneously. McLandress and Raveling (1981) found that storage of lipid reserves on the wintering area in Giant Canada Geese (*Branta*

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[2] Prepared for submission to the *Auk* as Schamber, J. L., J. S. Sedinger, D. H. Ward, and K. R. Hagemeier. Effects of winter location on reproductive performance of Pacific Black Brant.

canadensis maxima) is age-dependent; older females begin storing nutrients earlier in spring than 2-year-old females. Vangilder et al. (1986) suggested that reserves acquired on the wintering grounds by Atlantic Brant (*Branta bernicla hrota*) might directly affect migration and subsequently reproduction. Thus, levels of nutrient acquisition on the wintering areas may substantially influence migratory behavior and subsequently individual reproductive performance.

Heitmeyer and Fredrickson (1981) and Raveling and Heitmeyer (1989) used regression approaches to link winter habitat conditions to reproductive performance at the population level in Mallards (*Anas platyrhynchos*) and Pintails (*Anas acuta*). The difficulties of following individuals throughout an annual migratory cycle, however, have made it difficult to link reproductive performance of individuals to wintering areas they used. Long-term marking and monitoring programs of Pacific Black Brant (*Branta bernicla nigricans*) throughout their annual cycle enabled us to directly examine the relationship between winter location and reproductive performance.

Black Brant (hereafter brant) are among the smallest arctic-nesting geese (Owen 1980) and winter in intertidal and subtidal habitats along the Pacific Coast of North America from Alaska to Mexico (Bellrose 1980, Reed et al. 1998a). Diet outside of the breeding season is comprised almost entirely of relatively low quality seagrasses and marine algae (Einarsen 1965, Ward and Stehn 1989), and grazing opportunities are restricted to certain segments of tidal cycles (Kramer et al. 1979, Ward and Stehn 1989). Feeding constraints and poor quality diet (Reed et al. 1998a) may limit individual storage of nutrient reserves before the breeding season. Spatial variation in habitat quality,

therefore, may influence winter distribution of brant, thus promoting variation in reproductive performance among individuals using different winter locations.

Mid-winter surveys have indicated a northward shift in distribution of brant within Baja California in the past two decades; birds are shifting, for unknown reasons, to areas where they are harvested and where populations are denser (Conant et al. 1998). Shifts in winter distribution also have been documented in other brant goose populations. For example, geographic differences in harvest pressure altered distribution of Dark-bellied brant (Ebbinge 1991), and changes in distribution of Atlantic brant were likely in response to food availability (Kirby and Obrecht 1982). Wilson and Atkinson (1995) also linked use of Willapa Bay in Washington State, by wintering brant, to eelgrass abundance. Changes in distribution such as the one observed in Baja California may occur because of shifting balances between survival and fecundity (Raveling 1978) among birds from different locations or might represent behavioral responses to changing food abundance (Bellrose 1980, Kirby and Obrecht 1982, Vickery et al. 1995, Summers et al. 1996).

Human disturbance and habitat degradation currently threaten key wintering habitat in Mexico. Threats include increased recreational and residential development, shellfish farming, salt-mining, and stochastic events (Ward et al. 1993, Reed et al. 1998a). Most migration and wintering areas in the United States already have been impacted by development and industrialization (Barnhart et al. 1992, Wilson and Atkinson 1995, Reed et al. 1998a). For example, eelgrass beds along the western coast of the United States have been severely damaged or altered through shellfish farming

practices (Einarsen 1965, Wilson and Atkinson 1995). Given the potential importance of wintering areas for reproduction in geese, it is essential that we increase our understanding of the significance of these areas to individuals and ultimately to the dynamics of goose populations.

We observed individuals from the Tutakoke breeding colony during winter to examine variation in reproductive performance among individuals using different winter locations. Female nutrient reserve levels were measured using an index of their mass at hatch, and we compared reproductive performance of females using different winter locations by assessing the relationships between winter location and initiation date of clutches, clutch size, and probability of breeding the following season.

METHODS

STUDY AREAS

Breeding area. The current study is part of a long-term research project examining population ecology and demography of the Tutakoke River Black Brant colony on the Yukon-Kuskokwim Delta, Alaska (Sedinger 1993; Figure 2-1). The colony is situated at the confluence of the Tutakoke and Kashunuk Rivers (61°15'N, 165°37'W), 20 km south of Old Chevak, a U.S. Fish and Wildlife Service field station. The Tutakoke area is characterized by low salt marsh communities intersected by tidal sloughs, ephemeral ponds, and mud flats (Kinchloe and Stehn 1991). Brant nest in wet sedge meadows, dominated by tall *Carex spp.*, within 1 km of the Bering Sea coast. Following nesting, adults lead their broods to nearly homogenous grazing lawns, consisting primarily of *Carex subspathcea* and *Puccinella phraganodes*.

Approximately 35% of the 5,000 nesting pairs are currently marked with uniquely coded alphanumeric color tarsal bands. Capture-recapture analysis using the robust design (Nichols and Kendall 1995), indicates that we detect about 66% of 2-year-old females and 76% of ≥3-year-old females that are present on the colony each year (Sedinger et al. in press). We identify >1000 uniquely color-marked nesting pairs annually on the breeding grounds, which, coupled with high detection probability, enhances our ability to assess breeding probability and other reproductive parameters for brant from known winter locations.

Wintering areas. Nearly half of the brant population winters in embayments on the Pacific coast of Baja California; the remainder winters in bays along the west coast mainland of Mexico and along the Pacific coast of North America as far north as Alaska (Sedinger et al. 1993). Marked individuals were identified in seven distinct winter locations: San Ignacio Lagoon, Ojo de Liebre Lagoon, and San Quintin Bay, Baja California; Morro Bay and Humboldt Bay, California; Padilla Bay, Washington; and Boundary Bay, British Columbia.

Site fidelity is high on wintering areas (Ward et al. 1993, Reed et al. 1998b) allowing accurate determination of site use of females within years. However, brant experience protracted fall and spring migratory movements (Reed et al. 1998a); thus, it was necessary to establish a criterion for completion of movement into terminal winter locations and for initiation of spring movements. We used winter re-sight data only for individuals that were observed in more than one area to count the total number of initial band re-sightings of individuals in specific locations over ten-day periods across winter

months. During each ten-day period, proportions of initial re-sightings for each winter location were plotted, and relative numbers of new re-sightings were used as indicators of movement among areas. Because new bands were continually re-sighted throughout a ten-day period, consecutive periods with proportionally lower numbers of new band observations were indicative of minimal movement into an area, relative to periods with higher or increasing numbers of new band re-sightings. Therefore, individuals re-sighted in an area within these periods were assumed to have wintered in that location. Under these criteria, we were able to define distinct wintering periods for four locations: Boundary Bay, British Columbia; San Quintin Bay, Ojo de Liebre Lagoon, and San Ignacio Lagoon, Baja California (Figure 2-1). Individuals re-sighted in these areas during the defined wintering period were included in our analysis.

San Ignacio Lagoon was the second largest and southern-most (26° N, 112° W) of the three embayments sampled in Baja California. Based on patterns of appearance of new bands, we defined the winter period at San Ignacio as 7 January to 16 February. Density and abundance estimates of seagrass were lowest here among the three embayments (D. Ward unpubl. data). Ojo de Liebre Lagoon (27° N, 113° W), the largest of the three embayments, is located approximately 100 km north of San Ignacio Lagoon and contained the greatest number of brant (Conant et al. 1998). Dates defined for wintering brant at Ojo de Liebre Lagoon were similar to those of San Ignacio Lagoon. Density of forage was similar to San Ignacio Lagoon, but overall abundance of seagrass was greatest among the three areas given the areal extent of this lagoon (D. Ward unpubl. data). San Quintin Bay (30° N, 115° W) is located 300 km north of Ojo de Liebre

Lagoon and was the smallest of the three areas (D. Ward unpubl. data). This bay supported the highest density of wintering birds and seagrass in Baja California (D. Ward unpubl. data) and serves as a staging area during spring and fall migration (Ward et al. 1993, Reed et al. 1998a). We defined wintering dates at San Quintin Bay as 8 December to 5 February. San Quintin Bay was the only area with sport harvest in Baja California (Ward et al. 1993) during the study period. Boundary Bay, British Columbia (49° N, 120° W), is located in the Strait of Georgia approximately 2000 km north of San Quintin. Dates of this wintering period at this site were defined from 1 November through 5 February. We do not have estimates of density and abundance of seagrass for Boundary Bay.

FIELD METHODS

Breeding. Females initiate nests at Tutakoke approximately 9-11 days after peak arrival (Lindberg et al. 1997). During initiation all nests within 50 randomly distributed 100 m diameter plots were searched every four days and monitored until hatch was complete in 1993 and 1998-2000. Additionally, during incubation and hatch, the study area was searched for nests associated with marked birds; nests were monitored from discovery until hatch. We recorded clutch size, egg measurements (Flint and Sedinger 1991), and hatch dates at each nest.

Females were trapped at their nest during hatch using bow-net traps (Sayler 1962). Trapped females were weighed (± 10 g) using spring scales. We measured wing length and body length using a metric ruler (each ± 1 cm), and mid-wing, head length, total tarsus, and culmen (each ± 0.1 mm) were measured using dial calipers.

During remigial molt, adults and goslings were herded into corral traps (Cooch 1953). Each was fitted with a metal U. S. Fish and Wildlife Service band and a unique alphanumerically encoded color tarsal band. We measured culmen and tarsus (± 0.1 mm) of captured individuals using dial calipers and weighed them (± 10 g for adults and ± 5 g for goslings) using spring scales.

Wintering. Color tarsus-marked brant were re-sighted by staff of federal and state agencies and private individuals during winters of 1992-93 and 1997/98 to 1999/2000. Individually marked birds were identified (re-sighted) throughout the winter months using variable power spotting scopes. During the 1992/93-winter season, 4,498 individuals were re-sighted in Baja California, and 9,811 individuals were re-sighted across the 1997/98 to 1999/2000-winter seasons. Data were not collected in 1998 at Ojo de Liebre Lagoon. Across the 1998-2000-winter seasons, 1,066 different individuals were observed in Boundary Bay, British Columbia. Data were not collected in 1993 at Boundary Bay.

STATISTICAL ANALYSES

We assessed whether breeding status of individuals was associated with winter location and year using a log-linear model and maximum likelihood ratio chi-square test of significance (PROC CATMOD; SAS 1999). We did not have data for all four-winter locations in all years. Therefore, the interaction of winter location and year was not estimable and was excluded from the analysis. We only included females banded at Tutakoke in the analysis to avoid problems associated with dispersal of males (Lindberg et al. 1998) and lower breeding detection rates for females from other colonies. We

estimated the frequency of birds observed breeding at Tutakoke (PROC FREQ; SAS 1999) and present results by winter location and year. Breeding frequencies, as presented below, are not adjusted for estimates of survival of individuals from winter locations to Tutakoke, estimates of breeding philopatry to Tutakoke, or detection probability of individuals at Tutakoke. We approximate actual breeding frequencies for females from each winter location for discussion below by dividing our initial estimates by estimates of female adult survival for brant from wintering areas to Tutakoke, female breeding fidelity to Tutakoke, and detection probability given presence at the Tutakoke colony. A mean seasonal estimate (0.920) of adult survival for early (0.988) and late (0.860) spring was used for the interval between observations on winter and breeding locations (Ward et al. 1997). We used the weighted average (Rexstad and Anderson 1988) from estimates of female permanent emigration during years 1986-1993 at Tutakoke (J. Sedinger unpubl. data) to arrive at a conservative estimate (0.805) of philopatry for our purposes. Estimates of detection probability (0.760) were taken from Sedinger et al. (in press).

We used the general linear model (PROC GLM; SAS 1999) procedure to compare variation in clutch size among individuals from different wintering areas. To account for sources of variation, our most general model contained winter location, year, age class, and initiation date. We removed variation in initiation date among years by setting peak initiation in each year to 0 and adjusting individual initiation dates relative to the peak of initiation. Because we did not have clutch size data for all years, areas or age classes in all years, the interactions of age class and year with winter location could not be estimated and were not included in the analysis.

Variation in initiation date of individuals from different winter locations was compared using a general linear model (PROC GLM; SAS 1999) including winter location, year, and age class. We did not have data for all years and all age classes within years; therefore, the interaction of these effects with winter location could not be estimated and were not included in the analysis. Initiation dates were estimated from hatch dates assuming a 24-day incubation period and that females began incubating on the second-laid egg (Bellrose 1980).

We compared maternal mass at hatch among winter locations to examine potential variation in nutrient reserve levels. To control for variation in body size, we performed principal component analysis (PCA), using the correlation matrix of three linear variables (total tarsus, head length, and wing length) to construct the first principal component (PC1) as an index to structural size (Alisauskas and Ankney 1987). We then regressed female mass at hatch on PC1 and used the residuals to compare females from different winter locations (Ankney and Afton 1988). Residuals from the regression of mass on PC1 scores were used in a general linear model (SAS 1999) to compare variation in female weight at hatch while controlling for structural size, year, and age class. Data were not collected for all areas in all years, and not all age classes were present in all years; therefore, their interaction with winter location could not be estimated and was not included in the analysis.

We used an information-theoretic approach to assess multiple statistical hypotheses. In analyses performed using least squares method of estimation, we identified the most parsimonious model from candidate models using Akaike's

Information Criterion (AIC) (Burnham and Anderson 1998) derived from the estimated residual sum of squares (RSS) specific to a model (Anderson et al. 2000). To adjust for small sample size in our analyses, we used a modified criterion (AIC_c) (Burnham and Anderson 1998). We generated candidate models from permutations of our most general model, selected *a priori*. We ranked models by the difference in AIC_c score (ΔAIC_c) between the best model (lowest score) and each candidate model. We report Akaike model weights (w_i) as evidence for the best model and the importance of model parameters (Anderson et al. 2000).

RESULTS

The proportion of individuals we observed breeding the following summer at the Tutakoke River colony varied among winter locations (χ^2=19.56, df=3, P<0.0002; Table 2-1) and among years (χ^2=11.78, df=3, P<0.008; Table 2-1). Birds wintering in Boundary Bay on average had a higher overall breeding probability (39%), followed by individuals from San Quintin Bay (28%) and San Ignacio Lagoon (25%). Relatively few females (20%) wintering in Ojo de Liebre Lagoon bred than those from other areas. Additionally, individuals wintering in Baja California were less likely to breed in 1998 and 1999 than in other years (Table 2-1).

The selected best approximating model describing variation in clutch size included year and the covariate initiation date (Model 1, Table 2-2). The second- and third-best models that included winter location and age class, respectively, competed well with Model 1, as evidenced by ΔAIC_c<2 (Table 2-2), providing some support for variation in clutch size among females of different ages and winter locations. Females

from San Quintin laid slightly smaller clutches than females from other winter locations. Mean clutch size of females from San Ignacio was approximately 0.19 eggs larger than mean clutch size of females from San Quintin, after controlling for year, age class, and initiation date (Figure 2-2).

A winter location term was in our best model and the top five models explaining variation in initiation dates (Table 2-3). Summed model weights across the top 5 models were 0.89, providing strong evidence that winter location is an important determinant of initiation date. Additionally, substantial evidence exists to support an effect of wintering latitude on initiation date among females (Table 2-3). The structure of Models 1 and 2 contained a quadratic term for winter location, with a summed model weight of 0.68, suggesting a quadratic trend in the data (Table 2-3). This quadratic trend is not predictive of winter locations outside of the four we considered. Our most general model (Model 2) competed well with Model 1, providing some support for variation in initiation date among years and age classes (Table 2-3). Females from San Quintin Bay initiated clutches approximately 1.5 and 2.0 days earlier than females that had wintered in Ojo de Liebre and San Ignacio lagoons, respectively (Figure 2-3). Likewise, females from Boundary Bay initiated clutches approximately 0.3 and 1.3 days earlier than females from the two most southern areas in Baja California (Figure 2-3). Differences in means are likely conservative because birds that initiate later likely have shorter incubation periods (Eichholz and Sedinger 1999), which would have compressed variation in estimated initiation dates among winter locations. Furthermore, three (1998-2000) of the

years in our study were considered late springs (Lindberg et al. 1997) also compressing variation in nest initiation dates among females.

To construct PC1, total tarsus, head length, and wing length were selected as they yielded the highest adjusted r^2 (r^2=0.42) when mass was regressed against PC1 in a step-wise approach, considering all six linear measures. The model selected as best fitting variation of female mass at hatch included year and age class (Table 2-4). Support for winter location was weaker as it appeared in lower-ranked models, but received some support (ΔAIC_c <7; Table 2-4). A slight pattern of heavier females from southern areas in Baja California than from San Quintin Bay is evident (Figure 2-4).

DISCUSSION

EFFECTS ON REPRODUCTIVE PERFORMANCE

Breeding probability. The northward shift by brant wintering in Baja California over the past two decades could be explained by poorer production of brant wintering in southern Baja California. Individuals from different winter locations subsequently bred at different rates, consistent with an hypothesis of spatial variation in fecundity proposed by Vangilder et al. (1986) for Atlantic Brant (*Branta bernicla hrota*). Our data suggest that, averaged across years, individuals from northern winter locations (Boundary Bay and San Quintin Bay) bred at a higher rate than those from southern locations (Ojo de Liebre Lagoon and San Ignacio Lagoon).

Variation in breeding probability among wintering locations was greatest during the El Niño winter of 1997-98. Brant in Baja California dramatically shifted their distribution northward in 1998 (Conant et al. 1998, Sedinger et al. 1999) likely because

of substantially reduced food availability in more southern winter locations (D. Ward unpubl. data). Reduced probability of breeding by brant at Tutakoke was consistent with patterns at three other colonies on the Y-K Delta; overall, the number of nests was about 20% lower in 1998 than in 1997 (Anthony 2001).

To calculate comparable breeding probabilities, we adjusted our relative estimates of presence in 2000 for survival from winter to breeding areas, detection probability, and permanent emigration and obtained *ad hoc* estimates of breeding frequency: 0.73 for Boundary Bay, 0.62 for San Quintin Bay, 0.41 for Ojo de Liebre Lagoon and 0.62 for San Ignacio Lagoon. We adjusted breeding frequency only for that year because other years during our study contained missing data (1993, 1998) or immediately followed an El Niño-Southern Oscillation event; thus breeding frequencies for 2000 most closely represent a typical breeding season. Our estimates approach and in one case are intermediate to estimates provided by Sedinger et al. (in press) for annual breeding probability of two-year-old (0.67) and older (0.90) female brant at Tutakoke, indicating our estimates of relative breeding probability are approximately correct.

Initiation date. Females that wintered in southern areas (Ojo de Liebre and San Ignacio) initiated clutches later than those that wintered farther north (Boundary Bay and San Quintin Bay). Later initiating birds produce goslings that grow at a slower rate and are less likely to survive their first year, consequently leading to a reduction in recruitment (Sedinger and Flint 1991, Sedinger et al. 1995, Choudhury et al. 1996). These individuals also become smaller adults that produce smaller clutches (Sedinger et al. 1995). Lower recruitment and breeding rates for brant wintering in southern Baja

California could reduce the growth of this segment of the population directly, or favor shifts in wintering area, thereby producing the observed shift in winter distribution in Baja California.

Clutch size/Mass at hatch. Clutch size of females that had wintered in the two southern areas in Baja California was slightly larger than for females from San Quintin Bay. Schamber (2001) observed a slight, although weakly supported, trend of larger individuals wintering in southern areas of Baja California. In this study, however, we did not detect substantial variation in maternal mass at hatch, after controlling for structural size, among individuals who had wintered in different locations, although a slight pattern of heavier females from southern Baja California possibly occurred. Females from southern areas in Baja California, thus, may be able to acquire comparable reserves along their spring migration route by prolonging staging and delaying nesting relative to those wintering farther north (Drent and Daan 1980). Individuals wintering in southern areas of Baja California may delay nesting in order to achieve a 'threshold' condition necessary for reproduction. Patterns of variation in initiation date, clutch size and maternal condition, as we observed, are consistent with this hypothesis.

WINTER LOCATION EFFECTS

We hypothesize that southern wintering areas may effectively be population sinks, partially maintained through immigration, and driven by forces such as social interaction. Dominant family groups (Boyd 1953, Raveling 1970, Black and Owen 1989) may occupy northern areas, thereby relegating subordinate family groups, paired individuals without young, and non-breeding individuals to more southern areas.

Human activities cannot explain current changes in distribution within Baja California. San Quintin Bay, the only area with significant hunting activity, was the most productive of the three areas monitored for brant. San Quintin Bay is also supporting increasing numbers of brant (Conant et al. 1998).

San Quintin Bay contains the highest densities of intertidal eelgrass, while southern areas in Baja California have lower densities, of largely subtidal eelgrass (D. Ward unpubl. data). Nutrient content of seagrass declines with decreasing latitude, although the pattern varies among years (D. Ward unpubl. data). Eelgrass, which is at the southern-most extent of its temperature range in Baja California (Saunders and Saunders 1981), was adversely affected by the El Niño-Southern Oscillation event of 1997-98 (D. Ward unpubl. data). Standing crop biomass was considerably lower in Ojo de Liebre and San Ignacio lagoons than in San Quintin Bay during the winter of 1997-98 (D. Ward unpubl. data). We hypothesize that spatial variation in habitat quality is influencing variation in subsequent reproductive capabilities of individuals wintering in these different locations. Differential uptake of nutrients by individuals wintering in different areas likely impacts their ability to store nutrients, thus affecting migratory behavior and reproductive performance.

Conservation. Continued development in Baja California is underway or planned for the near future (Reed et al. 1998a), which has the potential to significantly impact the winter distribution of brant and habitat quality in these embayments (D. Ward pers. comm.). Future management and research concerns should focus on the impact that forage quality and abundance have on the distribution and dynamics of these wintering

populations. Continued alteration of winter habitat through anthropogenic and stochastic events could negatively impact the Pacific Brant population.

Population dynamics. Winter location exposes individuals to varying habitat conditions and social interactions, likely influencing fitness (Cristol et al. 1999). Individuals wintering in southern Baja California may experience less available food and in some years lower quality food than those wintering farther north (D. Ward unpubl. data). Our findings suggest that individuals wintering in southern Baja California are less likely to breed and potentially have fewer recruited young than individuals wintering farther north. Variation in nutrient acquisition, coupled with winter distribution of individuals could substantially influence individual reproductive performance, and in turn, population dynamics through limitations of population growth in southern segments of the wintering population and/or support shifts in winter distribution.

Figure 2-1. Map of the location of Tutakoke breeding colony and winter locations included in this study.

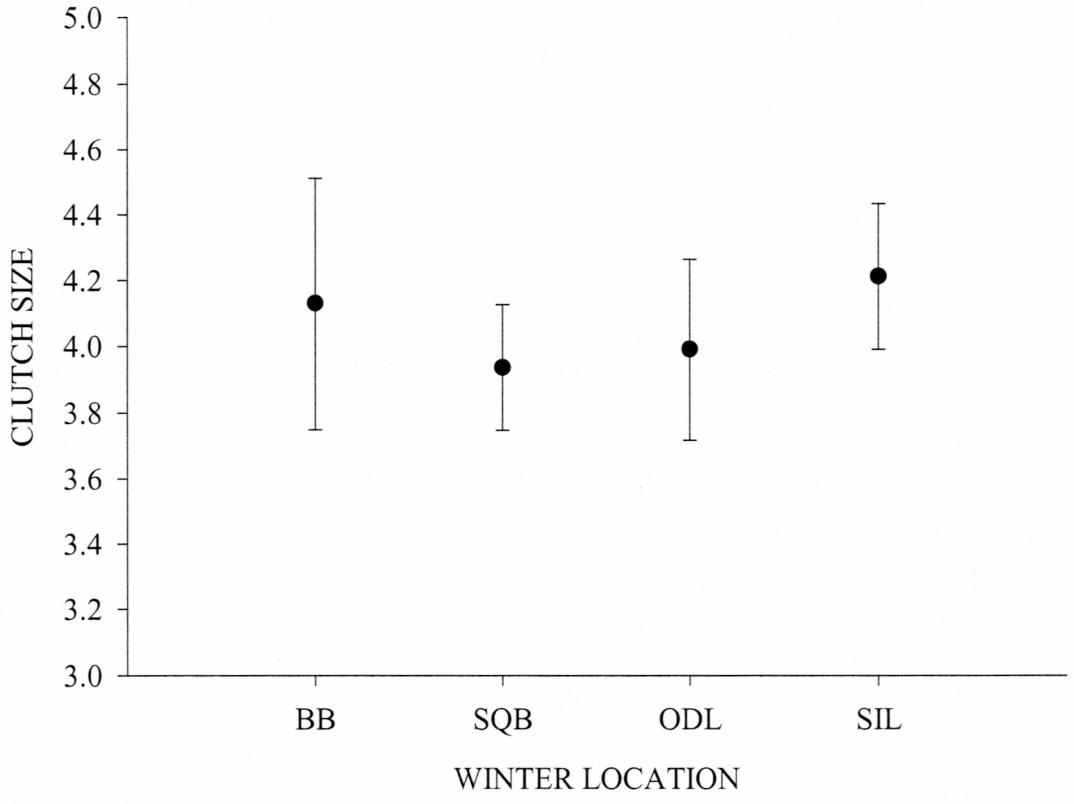

Figure 2-2. LSMean clutch size of individuals for each winter location, controlling for year, age class, and initiation date. Winter locations are arranged from north to south and abbreviated as: BB-Boundary Bay, SQB-San Quintin Bay, ODL-Ojo de Liebre Lagoon, and SIL-San Ignacio Lagoon. Error bars represent 1 SE from the mean.

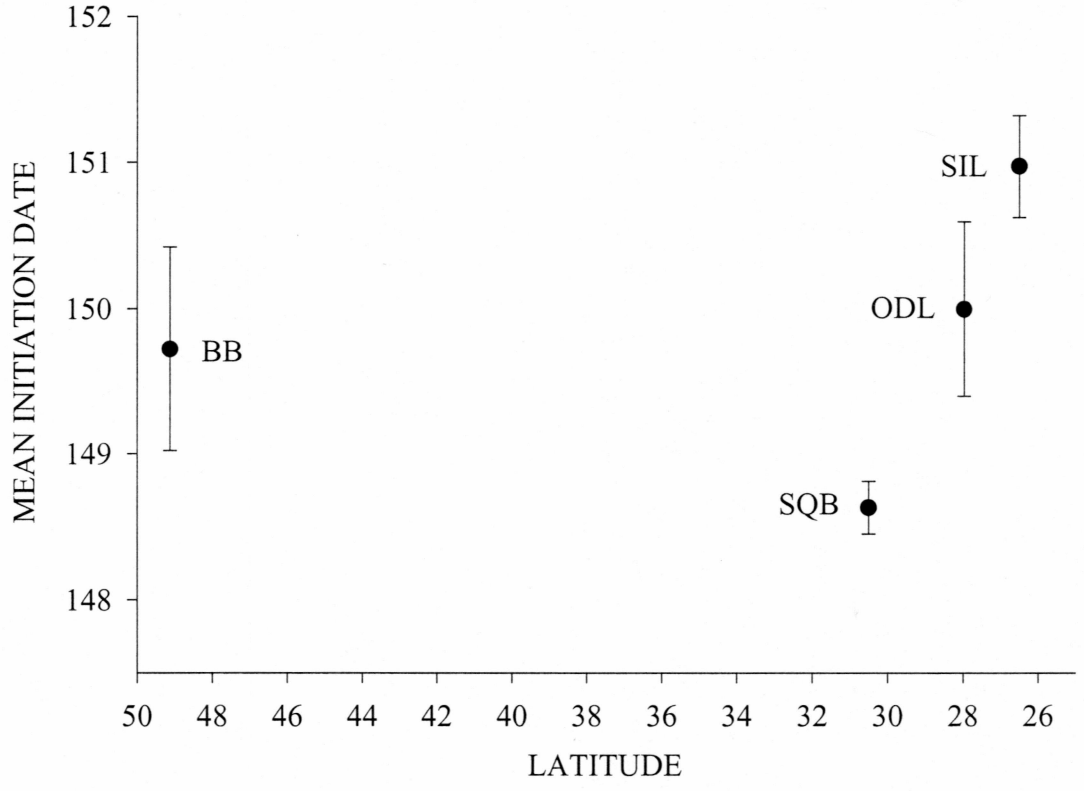

Figure 2-3. Mean initiation dates of clutches for individuals from each winter location, abbreviated as: BB-Boundary Bay, SQB-San Quintin Bay, ODL-Ojo de Liebre Lagoon, and SIL-San Ignacio Lagoon. Error bars represent 1 SE from the mean.

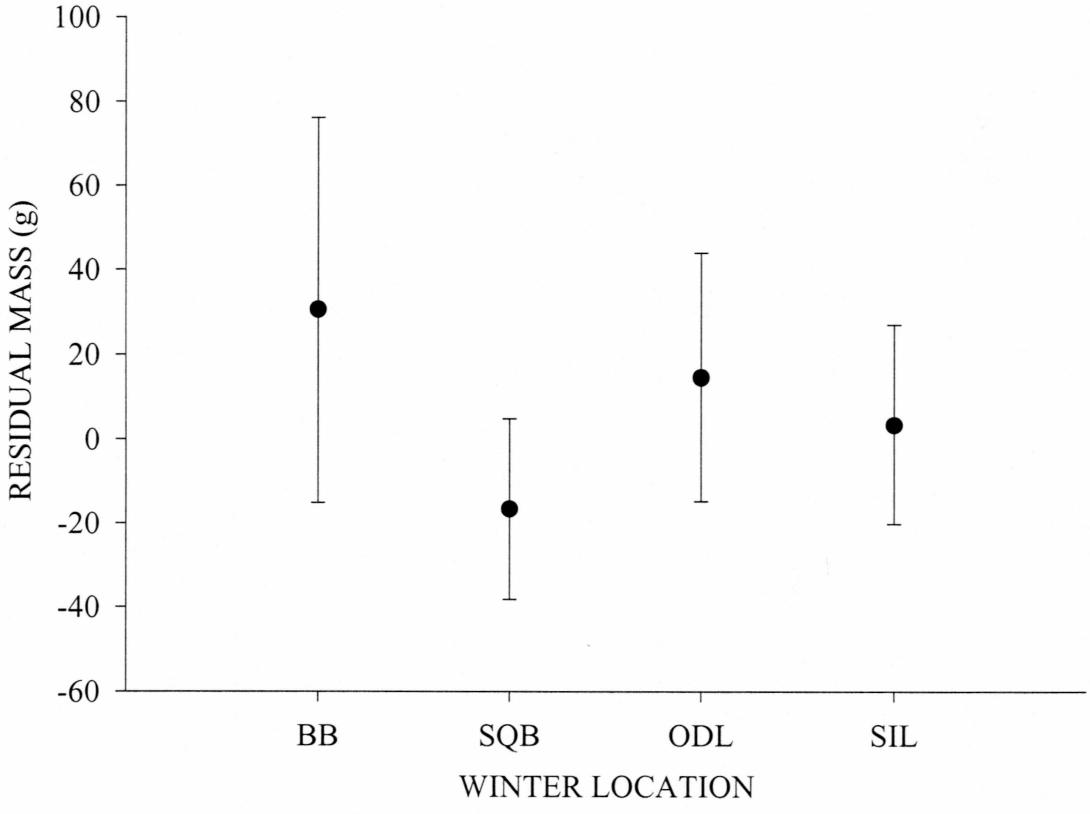

Figure 2-4. LSMean residual mass at hatch for females from each winter location, controlling for year, and age class. Winter locations are arranged from north to south and abbreviated as: BB-Boundary Bay, SQB-San Quintin Bay, ODL-Ojo de Liebre Lagoon, and SIL-San Ignacio Lagoon. Error bars represent 1 SE from the mean.

Table 2-1. Frequency of individuals breeding at Tutakoke from each winter location and in each year. Winter locations are arranged from north to south. Standard errors of estimates appear in parentheses.

	Winter Location				
Year	Boundary Bay	San Quintin Bay	Ojo de Liebre Lagoon	San Ignacio Lagoon	Totals
1993	NA	0.36 (0.04)	0.32 (0.10)	0.24 (0.11)	66
1998	0.36 (0.13)	0.23 (0.02)	NA	0.09 (0.04)	137
1999	0.46 (0.14)	0.30 (0.03)	0.14 (0.06)	0.27 (0.05)	92
2000	0.38 (0.13)	0.32 (0.03)	0.21 (0.05)	0.32 (0.05)	125
Overall	0.39 (0.08)	0.28 (0.01)	0.20 (0.03)	0.25 (0.02)	
Totals	17	308	28	67	420

NA indicates the absence of data from winter location in that year.

Table 2-2. Model selection criterion for clutch size variation in individuals from different winter locations during years 1993, 1998-2000.

No. and $Model_i$	SSE_i	K_i	AIC_c	Δ_i	w_i
1. {y i}	227.681	6	-25.598	0.000	0.359
2. {w i}	228.089	6	-25.127	0.470	0.284
3. {a i}	231.065	5	-23.812	1.786	0.147
4. {w y i}	225.049	9	-22.272	3.325	0.068
5. {y a i}	227.658	8	-21.386	4.212	0.043
6. {w a i}	227.720	8	-21.314	4.283	0.042
7. {y}	234.109	5	-20.370	5.228	0.026
8. {w y a i}	224.954	11	-18.043	7.555	0.008
9. {w}	236.614	5	-17.571	8.026	0.006
10. {a}	238.684	4	-17.358	8.239	0.005
11. {y a}	234.089	7	-16.187	9.411	0.003
12. {w y}	232.597	8	-15.740	9.857	0.002
13. {w a}	236.333	7	-13.678	11.920	0.000
14. {w y a}	232.567	10	-11.468	14.129	0.000

$Model_i$ parameters: y=year; w=winter location; a=age; i=peak initiation date

SSE_i=residual sum of squares from GLM of $model_i$

K_i=number of estimated parameters for $model_i$

AIC_c=modified Akaike Information Criterion score

Δ_i=difference of $model_i$ AIC_c score and top model (lowest AIC_c score)

w_i=Akaike model weight

Table 2-3. Model selection criterion for variation in initiation date of individuals from different winter locations during years 1993, 1998-2000.

No. and $Model_i$	SSE_i	K_i	AIC_c	Δ_i	w_i
1. {w y w^2}	1801.999	7	521.503	0.000	0.499
2. {w y a w^2}	1786.572	9	523.504	2.001	0.183
3. {w y}	1831.816	6	523.725	2.222	0.164
4. {y}	1856.367	5	525.145	3.642	0.080
5. {w y a}	1819.800	8	526.225	4.722	0.047
6. {y a}	1843.940	7	527.577	6.074	0.023
7. {w w^2}	2236.113	4	572.202	50.699	0.000
8. {w a w^2}	2203.524	6	572.499	50.995	0.000
9. {w}	2424.560	3	591.500	69.997	0.000
10. {w a}	2399.675	5	592.917	71.414	0.000
11. {a}	2452.462	4	596.583	75.080	0.000

$Model_i$ parameters: y=year; w=winter location; a=age; w^2=quadratic term

SSE_i=residual sum of squares from GLM of $model_i$

K_i=number of estimated parameters for $model_i$

AIC_c=modified Akaike Information Criterion score

Δ_i=difference of $model_i$ AIC_c score and top model (lowest AIC_c score)

w_i=Akaike model weight

Table 2-4. Model selection criterion for mass at hatch of females from different winter locations during years 1993, 1998-2000.

No. and $Model_i$	SSE_i	K_i	AIC_c	Δ_i	w_i
1. {y}	366858.172	3	673.339	0.000	0.440
2. {y a}	364149.256	4	674.974	1.635	0.194
3. {a}	375286.193	3	675.133	1.794	0.179
4. {w y}	351089.630	6	676.715	3.375	0.081
5. {w}	365471.862	5	677.542	4.202	0.053
6. {w y a}	349341.698	7	678.731	5.392	0.029
7. {w a}	363753.175	6	679.514	6.175	0.020

$Model_i$ parameters: y=year; a=age; w=winter location

SSE_i=residual sum of squares from GLM of $model_i$

K_i=number of estimated parameters for $model_i$

AIC_c=modified Akaike Information Criterion score

Δ_i=difference of $model_i$ AIC_c score and top model (lowest AIC_c score)

w_i=Akaike model weight

CONCLUSIONS

The northward shift in winter distribution over the past two decades by brant in Baja California may be a function of poorer production of brant wintering in southern areas of Baja California. Females wintering in southern areas in Baja California were less likely to breed than were individuals from northern locations. Furthermore, individuals from southern areas initiated clutches later than did individuals from northern areas. Later initiating brant produce slower growing goslings that are less likely to survive their first year, leading to a reduction in recruitment (Sedinger and Flint 1991, Sedinger et al. 1995, Choudhury et al. 1996). Those goslings that survive become smaller adults that lay smaller clutches (Sedinger et al. 1995).

We detected little variation in structural size and maternal mass at hatch among females using different winter locations, although a weakly supported latitudinal trend existed in Baja California. Individuals wintering in San Quintin Bay were structurally slightly smaller than those wintering in Ojo de Liebre Lagoon and San Ignacio Lagoon. Furthermore, clutch size was slightly larger in females wintering in southern areas in Baja California than those wintering in San Quintin Bay. This supports the Drent and Daan (1980) hypothesis, although weakly, that individuals in poorer condition may delay or extend migration to acquire reserve levels necessary to lay a larger clutch than otherwise possible. The negative consequence of such a decision, however, is delayed nesting, which we observed in individuals from southern areas.

The proportion of juveniles wintering in Baja California was higher in San Quintin Bay and Ojo de Liebre than in Boundary Bay and San Ignacio Lagoon, consistent with a hypothesis of variation in fecundity of pairs using different winter locations. Individuals from Ojo de Liebre Lagoon, however, were less likely to breed than those from other areas and initiated clutches later than individuals wintering farther north, suggesting that variation in fecundity cannot fully explain winter distribution in brant.

Spatial and temporal variation in food abundance and availability exists in Baja California (D. Ward unpubl. data). Density and availability of seagrass is higher in San Quintin Bay than in southern areas (Ojo de Liebre Lagoon and San Ignacio Lagoon) in Baja California. Furthermore, nutrient quality of seagrass appears to decline with latitude in Baja California, although this relationship varies among years (D. Ward unpubl. data). Additionally during the El Niño-Southern Oscillation event of 1998, the distribution of brant dramatically shifted northward into San Quintin Bay (Conant et al. 1998, Sedinger et al. 1999) likely a result of considerably lower standing crop of seagrass in Ojo de Liebre and San Ignacio Lagoon relative to that in San Quintin Bay (D. Ward unpubl. data). We suggest that spatial and temporal variation in winter habitat quality may be influencing distribution and the reproductive capabilities of individuals from different winter locations.

We hypothesize that southern winter locations in Baja California may be population sinks, partially maintained through immigration and driven by forces such as social dynamics. Dominant family groups (Boyd 1953, Raveling 1970, Black and Owen 1989) may occupy northern areas with more favorable foraging conditions (Raveling

1970, Teunissen et al. 1985, Black et al. 1992), thereby displacing subordinate family groups, paired individuals without young, and non-breeding individuals to less favorable southern winter locations. Lower recruitment and breeding rates for brant, that winter in southern locations in Baja California could reduce the growth of this segment of the breeding population at Tutakoke directly. Variation in nutrient acquisition, coupled with winter location of individuals, could substantially influence individual reproductive performance and consequently population dynamics through limitations of growth in populations wintering in different locations or support shifts in winter distribution.

Winter habitat for Pacific brant is currently influenced by human activities and climatic events such as commercial and residential development, shellfish farming, tourism, heavy siltation, and El Niño-Southern Oscillation events (Reed et al. 1998a, D. Ward unpubl. data). Continued alteration of habitats could severely impact distribution and population dynamics through increases in winter habitat variability, thereby influencing breeding propensity and fecundity. Our results support our hypothesis that winter locations affect reproductive performance; thus, future research should focus on the impact that winter distribution and habitat quality have on the dynamics of wintering populations.

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